Selbyana 22(2): 181–191. 2001.

SAMPLING METHODS FOR VASCULAR EPIPHYTES: THEIR EFFECTIVENESS IN RECORDING SPECIES RICHNESS AND FREQUENCY

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ABSTRACT. Vascular epiphytes are an important component of tropical biodiversity; however, because of problems associated with accessing them, it is hard to obtain a complete species inventory. It is faster and safer to make ground-based observations of epiphytes than it is to collect data using climbing techniques, but the quality of the observations may be suspect. To compare ground-based observations and observations based on climbing, we recorded epiphytic species present in three types of vegetation: remnant trees in pasture, a forest corridor along a brook, and a closed forest. Using species accumulation functions, we predicted total species richness and the sampling effort to determine it. Ground-based observations underestimated epiphytic species richness, but this underestimation was independent of vegetation structure and tree size. The number of epiphytic species recorded with climbing-based observations increased by 16.3–23.3% over the number recorded with ground-based observations. Such observations underestimated species frequency and could indicate that a species is rare when it is not. Species accumulation models fitted to ground-based data failed to predict species richness correctly. If fitted to climbing-based observations, however, they could predict the richness and sampling effort for a complete species inventory. Our study demonstrated the limitations and problems of ground-based epiphyte observations for species inventories.

Key words: canopy access, vascular epiphyte inventory, species richness, species accumulation functions, cloud forest

INTRODUCTION

Epiphytic plants are an important component of tropical biodiversity and the object of many local floristic inventories. In some tropical forests, vascular epiphytes may represent from one-third to one-half of total vascular flora (Gentry & Dodson 1987). Obtaining a complete inventory of epiphytes is difficult, however, because many species are small or rare; some have short flowering seasons; and many groups, such as *Peperomia,* are not taxonomically well known (Ingram & Lowman 1995, Hietz & Wolf 1996, Shaw & Bergstrom 1997). Although taxonomic conflicts could be resolved (even using morphospecies), the small size and seasonal flowering of many plants make careful and long-term sampling necessary. To obtain an accurate estimate of epiphyte species richness, an observer must consider vegetation structure, tree species richness, and bark and crown characteristics. Studies have suggested that a complete assessment of vascular epiphyte diversity requires sampling of the largest trees using species/area or species/tree-volume functions as well as sampling in different seasons of the year (Ingram & Lowman 1995, Hietz & Wolf 1996, Shaw & Bergstrom 1997).

Epiphyte records frequently are obtained using both ground-based observations and plants collected from fallen branches and trees (Ingram & Lowman 1995, Lowman & Wittman 1996). Although ground-based observations are rapid and safe, most plants found on the forest floor do not have reproductive structures; furthermore, vegetative structures may be different from those in the upper canopy, and ecological information could be lost (Ingram & Lowman 1995). Thus, most herbarium vouchers of epiphytes lack complete field data. For instance, less than 10% of vouchers in the Selby Botanical Gardens Herbarium (SEL) have ecological information on canopy habitat (Ingram & Lowman 1995).

Epiphytes in a simple-structured forest (with the tallest trees less than 20 m and without shrubs and vines) may be observed from the forest floor (Shaw & Bergstrom 1997). In taller and more complex forests, however, climbing host trees is recommended (Hietz & Wolf 1996, Shaw & Bergstrom 1997). Tree-climbing techniques have been developed only recently (Perry 1978, Perry & Williams 1981, Moffett & Lowman 1995, Barker 1997, Brockelman 1997). Such techniques require special training and are time consuming, but they allow researchers to gather information about the microhabitats of each species and possible species associations. Tree climbing also provides access to vegetative and reproductive plant material from the upper

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canopy (Ingram & Lowman 1995, Hietz & Wolf 1996). For example, the number of epiphytic species recorded for the Monteverde cloud forest in Costa Rica has increased more than 15% with intensive sampling accomplished by tree climbing (Ingram & Lowman 1995).

The suitability of ground and climbing observations may depend on forest structure and the purpose of the research. At present, however, no comparative studies have evaluated their accuracy for epiphyte inventories. Recognizing the merits of each method can facilitate comparison of different epiphyte inventories and serve as the basis for future epiphyte surveys. Here, we report epiphyte species numbers obtained from ground observations and tree climbing in three types of vegetation: a remnant forest, a forest corridor along a brook, and isolated trees in pasture. For both ground-based and climbing-based observations, we compared the species richness inventory obtained, the effect of vegetation structure on epiphytic record, the ability to record rare species, and the completeness of the inventory using species accumulations functions.

Study Site

The study was carried out in an area of montane cloud forest in San Andrés Tlalnelhuayocan, near Xalapa, Veracruz, Mexico (19°30′56″N, 96°59′50″W; 1500–1600 m above sea level). Mean annual precipitation is 1440.5 mm and mean annual temperature is 18°C (García 1964). The area has been disturbed and the present landscape includes remnant-closed forest fragments (forest), narrow forest corridors left along brooks (riparian), and isolated trees in pastures (Zamora 1992). Dominant trees in the forest were *Quercus* spp. (Fagaceae) with an importance value (IV) of 55.8 (Brower & Zar 1977) and *Liquidambar macrophylla* Oerstd. (IV = 13.3, Hammamelidaceae). Dominant riparian trees were *Platanus mexicana* (IV = 32.4, Platanaceae) and *L. macrophylla* (IV = 27.5); and dominant pasture trees were *L. macrophylla* (IV = 63.9), and *Quercus* spp. (IV = 16.2) (A. Flores-Palacios unpubl. data). Canopy complexity increases from pasture trees to forest trees. In the pasture, which has no shrubs or vines, mean tree height is 27 m (35 m maximum), tree density is low (1.7 trees/ha), and tree trunks and crowns can be easily observed with binoculars. In riparian forest, which has vines but no shrubs, tree height is similar to that of pasture trees, while tree density is higher (35 trees/ha). Not all trunks and crowns could be observed from the ground. In the forest, which has shrubs and vines, trees are the tallest (mean 33 m, maximum height 45 m) and tree density is the highest (163 trees/ha) of all areas, making ground observations very difficult.

Methods

Fieldwork was conducted in July and August of 1997 and 1998. In 1997, we recorded all species of vascular epiphytes on trees (dbh $\geq$ 30 cm, height $\geq$ 12 m) from the forest floor using binoculars (Pentax PCF 7 $\times$ 50, 6.2° and Nikon 8 $\times$ 23, 6.3°). The same trees were climbed in 1998 using single rope techniques (Perry 1978), and all epiphyte species were recorded again. In pasture, all 17 trees present on ca. 10 ha were sampled; in riparian forest, all trees contained within two plots (42 trees, ca. 1.2 ha.) were sampled; and in forest, all trees present in three 10 $\times$ 100 m transects (49 trees, ca. 0.3 ha.) were sampled. Epiphyte species were identified using field guides (Hietz & Hietz-Seifert 1994), and herbarium vouchers were deposited at the Herbarium of the Instituto de Ecología, A.C. (XAL). Where new or old reproductive structures were present, we recorded only adult plants.

Species Richness Inventory

We defined total epiphytic species richness (100%) as the total number of species recorded by climbing observations for all vegetation types studied. To evaluate the increase in species richness with the climbing technique, we calculated the difference between number of species by climbing and by ground observations.

Effect of Forest Structure

If forest structure is a factor influencing the accuracy of a method, then we should expect that the number of epiphytes added by climbing would increase from pasture to forest in accordance with tree size. We therefore performed a covariance analysis (GLIM 4; Francis et al. 1993), using vegetation type (pasture, riparian, and forest) as a factor in the model, tree size (basal area) as a co-variable, and species number added per tree/vegetation as the response variable. Since the response variable was counted, we used a Poisson Error Model with a logarithmic link function. We rescaled the final model to overcome over-dispersion problems (cf. Crawley 1993).

Rare Species Detection

Rareness is measured as the frequency of a species on each sampling unit (tree) (Hietz & Wolf 1996, Butler & Chazdon 1998). We de-

TABLE 1. Observed and predicted epiphyte species richness in three vegetation types sampled using two methods. Richness predictions were estimated calculating the asymptote of two species accumulation models.

Vegetation type	Observed species richness	Predicted species richness	
		Clench model	Linear dependence model
Ground-based observations			
Pasture	33	39	31
Riparian	67	79	64
Forest	66	78	63
Climbing-based observations			
Pasture	43	48	41
Riparian	80	90	75
Forest	81	90	76

fined a rare species as one present on less than 10% of the trees sampled. We calculated the probability of detecting rare species from the ground and by climbing. After conducting both observation methods, we recorded species previously labeled as rare that remained so and also new rare species.

Species Accumulation Functions

When time and budget are limited, ground-based observations may be the only option, but their accuracy must be questioned. Species accumulation functions can estimate total species richness and the richness percent recorded to date (Colwell & Coddington 1994). Thus these functions can measure the accuracy of ground-based and climbing-based observations, if sampled size remains equal. If ground-based observations were as accurate as climbing-based observations, then we expected predicted richness to be identical according to ground and climbing observations. Using trees as units of sampling effort, we constructed a mean species accumulation curve for each vegetation type and recording method. Curves were constructed by randomizing the sample order 500 times using EstimateS Software (Colwell 1997). Different-sized sample units (trees) were thus homogenized, and we avoided the jumps in accumulation curves occasioned by the biggest trees or trees having a greater number of unique species (species appearing once). We fitted the Clench and the Linear Dependence models (Soberon & Llorente 1993) to the mean curves obtained.

The Clench model assumes that the probability of adding new species to the inventory decreases with a heightened sampling effort but may increase as the observer gains experience. The Linear Dependence model assumes that as the inventory grows, the probability of finding new species decreases in a linear pattern (Soberón & Llorente 1993). In both models the calculated asymptote, an estimation of real species richness, is used to evaluate the completeness of the inventory (Soberon & Llorente 1993, Colwell & Coddington 1994, León-Cortés et al. 1998). We also calculated the sampling effort (number of trees to sample) required to obtain 90% of the asymptote. For the Clench model, we used the Soberon and Llorente (1993) equation $tq = q/[b(1 - q)]$; for the Linear Dependence model, we used the Lamas, Robbins and Harvey (1991) equation $tq = -1/b \ln(1 - q)$. In both equations, tq is the sampling effort needed to obtain the q proportion of the asymptote, and b is the slope. We used non-linear regression procedures to fit the two models to the mean curves (Mitchell & Bostrom 1992–1994).

RESULTS

Species Richness Inventory

We found 101 species of vascular epiphytes among the three types of vegetation studied (APPENDIX). TABLE 1 shows the species numbers found in each vegetation type by each sampling method used. With climbing observations, we added 10, 13, and 15 species to the list of species obtained by ground-based observations for pasture, riparian, and forest environments, respectively (TABLE 1). This means that recorded epiphytes based on ground observations represent only 77% of the total species recorded by climbing observations in pasture, 84% in riparian, and 82% in forest. Additionally, ground-based observations underestimated the frequency of another 21 species in pasture, 32 in riparian, and 43 in forest. In other words, from 56% (riparian) to 72% species (pasture and forest) were unrecorded or their frequency underestimated using ground-based observations.

TABLE 2. Mean number of epiphyte species per tree (mean ± SE) using ground- and climbing-based observations and mean number of species added with climbing. Values in parentheses are minimum and maximum.

Vegetation type	Ground-based observations	Climbing-based observations	Species added with climbing
Pasture	10.2 ± 1.0 (5–24)	17.0 ± 0.9 (7–32)	5.2 ± 0.8 (1–12)
Riparian	10.9 ± 0.7 (3–26)	15.6 ± 0.7 (5–27)	4.7 ± 0.4 (1–10)
Forest	11.8 ± 0.8 (3–27)	16.2 ± 0.5 (5–35)	5.2 ± 0.5 (1–18)

Forest Structure Effect

TABLE 2 shows mean (±SE) species number per tree recorded with both sample methods and mean number of species added with climbing. The latter figure did not differ between vegetation types ($F = 0.60$, d.f. = 2, 102, $P = 0.54$; TABLE 2). Nor was there a relationship between the number of species added by climbing and tree size ($F = 2.43$, d.f. = 1, 102, $P = 0.12$; FIGURE 1).

Rare Species Detection

Based on ground observations, 15 species in pasture, 39 in riparian, and 39 in forest were classified as rare, while climbing observations indicated 16, 32, and 34 rare species, respectively (TABLE 3). Although these figures may seem similar, important differences are noted. Several species considered as rare from ground-based observations were actually common, while others (7 in pasture, 8 in riparian, and 12 in forest) were recorded and categorized as rare by the climbing method. Probabilities of correctly classifying a species as rare from ground-based observations were 56% in the pasture, 80% in riparian, and 74.6% in forest.

Species Accumulation Functions

Mean species accumulation curves and fitted models are shown in FIGURES 2 and 3. Both

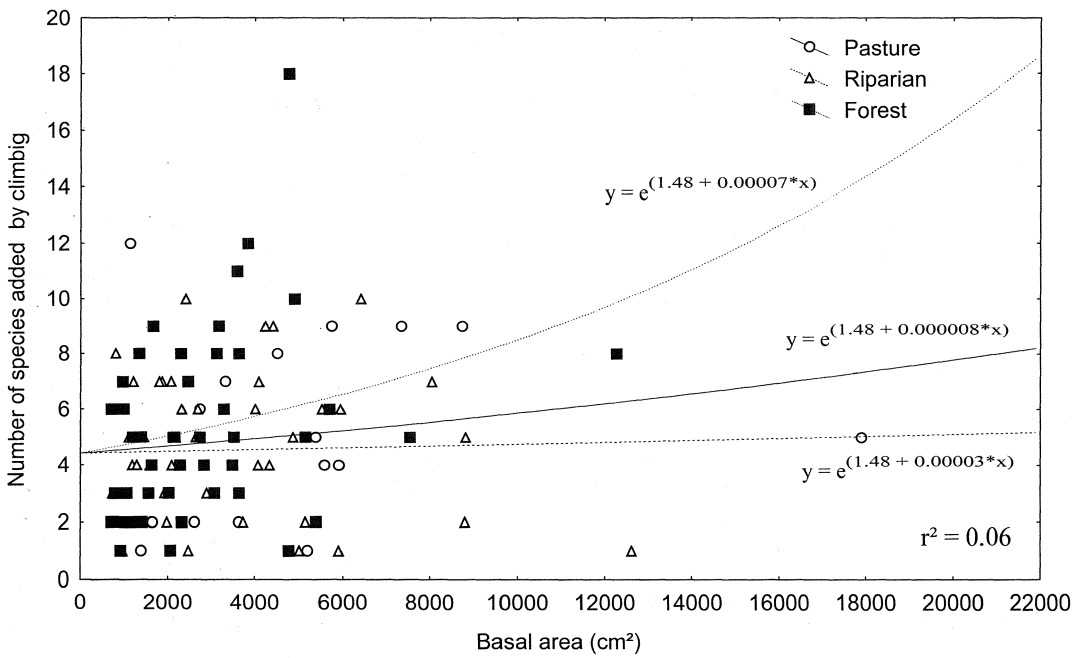

FIGURE 1. Relationships between tree size (basal area) and number of epiphyte species per tree added by climbing observations in three vegetation types.

TABLE 3. Number of rare species obtained with ground- and climbing-based observations. Incorrect species are those considered rare with ground-based observations but found to be more abundant with climbing method.

	Ground-based observations		Climbing-based observations
Vegetation type	Rare species	Incorrect species	Rare species
Pasture	15	6	16
Riparian	39	7	40
Forest	39	5	46

models fit the mean curves well (all $r^2 > 0.96$). In general, species richness as predicted by the Clench model was substantially higher than that predicted by the Linear Dependence model (TABLE 1). Species richness as predicted by the Linear Dependence model was lower than the species richness recorded with both sampling methods (TABLE 1). Thus the Linear Dependence model underestimated species richness and suggested that the species inventory was already complete.

For all vegetation types, the Clench model predicted superior species richness than was observed (TABLE 1). Species richness as predicted by the Clench model, however, was different for the two recording methods: when fitted to ground records, it predicted less species than when fitted to climbing-based observations (TABLE 1). Surprisingly, using the Clench model, the numbers of species predicted with ground-based observations were similar to those recorded with climbing-based observations (TABLE 1). For example, in riparian we observed 80 species by climbing, and the Clench model predicted 79 species (98.7%).

The Clench model estimated that inventory completeness would range from 89% (riparian) to 90% (pasture and forest), using climbing-based observations (TABLE 4).

The models differed in the minimum number of sample trees required to obtain 90% of the predicted species richness (asymptote). Ninety percent of the species richness estimated by the Linear Dependence model was obtained with half of the trees sampled in this study (TABLE 4). The Clench model estimated that this proportion of the asymptote could be obtained by increasing sample size from 30% to 50% with ground-based observations and from 55% to 141% with climbing-based observations (TABLE 3).

DISCUSSION

The climbing-based method was better for recording vascular epiphytes than was the ground-based method. The total canopy access possible with the former method allowed observation of species not seen from the ground. Shaw and Bergstrom (1997) suggested that epiphytes in a simple-structured forest might be observed from the forest floor; however, our data do not support this hypothesis. With the climbing method, the highest increase in percentage of species was found in the simplest type of vegetation (pasture) and the lowest in the most structurally complex type of vegetation (forest). Furthermore the mean number of epiphyte species added by the climbing method was unrelated to tree size; other vegetation characteristics may be responsible for this pattern. Tree architecture is different in pasture and forest. Isolated trees (pasture) have lower and more numerous branches than do forest trees, making ground-based observations more difficult. In the forest, however, high-

TABLE 4. Number of sampled trees from the three vegetation types studied and effort (as number of trees) needed to reach 90% asymptote using two species accumulation models (Clench and Linear Dependence) and two epiphyte observation methods.

		Estimated number of trees to reach 90% of asymptote	
Vegetation type	Number of trees sampled	Clench model	Linear dependence model
Ground-based observations			
Pasture	17	34	9
Riparian	42	89	24
Forest	49	79	23
Climbing-based observations			
Pasture	17	24	8
Riparian	42	71	20
Forest	49	63	20

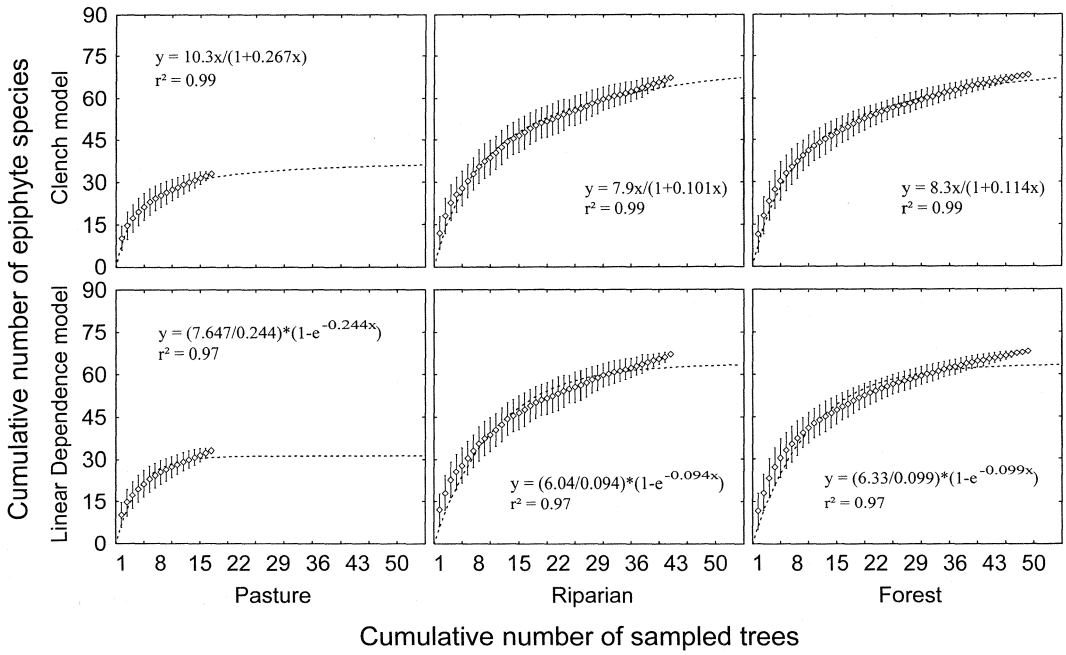

FIGURE 2. Mean species accumulation curves of epiphytes recorded by ground-based observation in three vegetation types. Mean curves are based on 500 randomized sample (tree) orders. Fitted curves predicted by the Clench and Linear Dependence models are shown. Error bars are standard deviations.

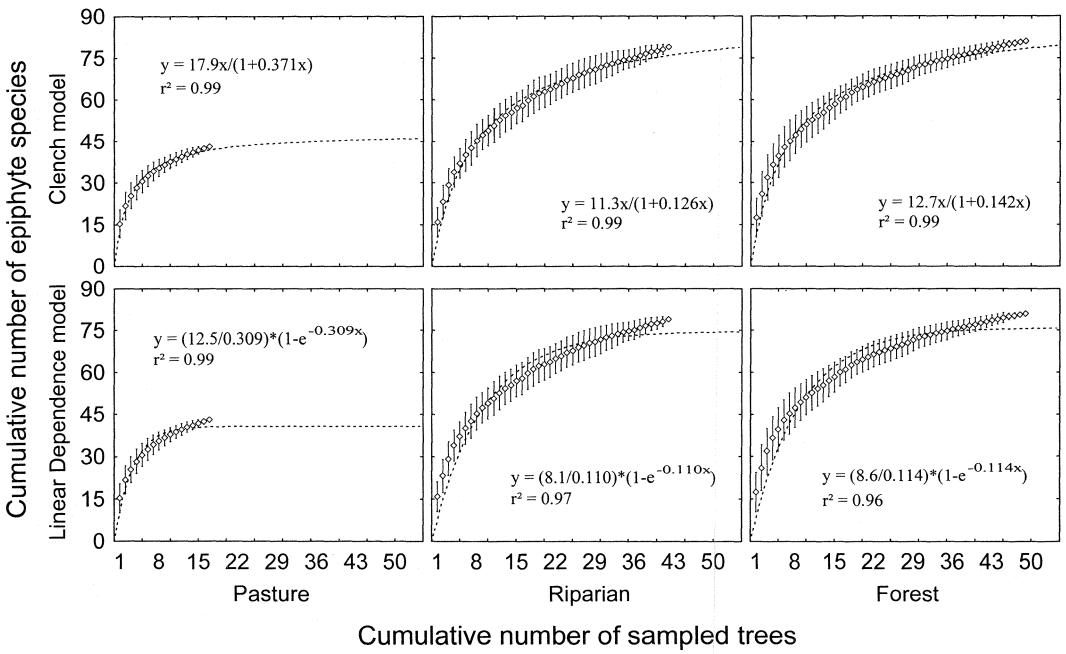

FIGURE 3. Mean species accumulation curves of epiphytes recorded by climbing-based observation in three vegetation types. Mean curves are based on 500 randomized sample (tree) orders. Fitted curves predicted by the Clench and Linear Dependence models are shown. Error bars are standard deviations.

er tree density and shrubs and vines could have the same effect as lower branches in isolated trees. Epiphyte density is, in contrast, higher in pasture than in forest, where trees carry 4.2 ± 0.8 kg/m^2 of mean dry epiphyte biomass, while pasture trees have 8.0 ± 0.8 kg/m^2 (A. Flores-Palacios unpubl. data). Big clumps of bromeliads, ferns, and aroids hide small and low-density plants (e.g., some orchids and *Peperomia*), and the climbing method allows us to record those plants.

Truly rare species were not observed using ground-based techniques. Although plant size is an important factor in rare plant detection, it is not the only one to take into account. With ground-based observations, we underestimated the frequency of some medium-sized plants (30–50 cm maximum size; see APPENDIX). Examples include *Catopsis nitida* (Hook.) Griseb. (Bromeliaceae), *Prosthechea vitellina* (Lindley) W.E. Higgins (Orchidaceae), (both from pasture and riparian), and *Tillandsia juncea* (Ruiz & Pav.) Poir. (Bromeliaceae) (from pasture and forest). The frequency of plants as large as 1 m also was underestimated (see APPENDIX). Examples include *Acineta barkeri* (Bateman) Lindl. (Orchidaceae) (forest) and *T. ghiesbregthii* Baker (riparian). Rare huge plants such as *Epidendrum parkinsonianum* Hook. (Orchidaceae), *T. foliosa* M. Martens & Galeotti, and *T. limbata* Schltdl. were recorded only with climbing-based observations. This suggests that ground-based observations could underestimate the frequency of plants even taller than 30 cm. Consequently, ground-based inventories may be incomplete and rare species inclusions could be a mistake.

Ground-based observations could not be used to estimate total species richness both because inventory size was underestimated by the Linear Dependence model (TABLE 1) and because predicted richness per the Clench model (TABLE 1) was similar to that observed by climbing. These findings are nevertheless a validation of species richness values as predicted by the Clench model. Apparently with the superior sampling method (climbing), the model would predict total richness accurately. As in other biodiversity surveys, however, model prediction validity also depends on researcher experience and knowledge of the group sampled (e.g., Soberón & Llorente 1993, León-Cortés et al. 1998, Butler & Chazdon 1998). This is the first time that such validation has been made using field data.

The Clench model and climbing-based observations indicated that the minimum sampling effort needed to reach 90% of the inventories is 24 trees in pasture, 71 in riparian, and 63 in forest. Possibly the remaining epiphyte species predicted are either on the smaller, non-sampled trees or are part of the inherent error in epiphyte sampling. In the three vegetation types studied, the smallest trees (dbh $<$ 30 cm, height $<$ 3 m) support several epiphyte species (A. Flores-Palacios unpubl. data). These smallest non-sampled trees increase the inventory to 50 species in pasture and 94 in forest, only two and four species more than the values predicted by the Clench model (TABLE 1), respectively. In the riparian site, the smallest non-sampled trees increase the epiphyte inventory (82 species), but below the value predicted by the Clench model (TABLE 1). In the riparian, the inherent sampling error could explain epiphyte over-estimation. Epiphyte-sampling sources of error include inconspicuous plants growing near plants that are bigger or immature. The former problem can be solved by sampling a greater number of trees, which increases the probability of finding inconspicuous plants. After sampling all trees in the riparian site, we concluded that over-estimation of predicted richness was the result of an error caused by the presence of immature plants and that the model's predictions could be values predating forest fragmentation.

Development of epiphyte records using the ground-based method is cheaper, safer, and more efficient (more trees by day), but inconspicuous or infrequent species may be overlooked (Lowman & Wittman 1996, Shaw & Bergstrom 1997). Additionally ground-based records are not useful in predicting species richness through species accumulation functions. Climbing methods, on the other hand, allowed us to record almost all epiphytic species present on sampled trees in any type of vegetation and to obtain ecological data for the canopy. Climbing also is useful in predicting species richness with species accumulation functions. Our results indicate that, when possible, climbing observations should be used in lieu of ground-based methods for recording epiphyte species.

ACKNOWLEDGMENTS

We thank Claudia Moreno for help with species accumulation function analysis. M. Palacios-Ríos and K.V. Melthreter (ferns) and P. Hietz (Araceae, Piperaceae, Bromeliaceae) helped us with species determination. D. Martínez B., J. Flores, V. Vázquez, E. Martínez, L. Cruz, J. Tolome, and R. Márquez provided help during fieldwork. L. Eguiarte, J. Villalobos, P. Hietz, J. Wolf, R. Ortíz-Pulido, A. Muñoz-Alonso, V. Rico-Gray, A. Cruz-Angón, and S. Valencia made comments and suggestions on an early draft. H.J.F. van Dunné, B.K. Holst, two anonymous reviewers, and translator I. Márquez improved the manuscript. The research was sup-

ported by the Instituto de Ecología, A. C., (902-16) and CONACYT (grant No. 1840P-N to García-Franco and scholarship No. 95019 to Flores-Palacios). This study constitutes part of the doctoral research in Ecología y Manejo de Recursos Naturales by A. Flores-Palacios at the Instituto de Ecología A.C.

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APPENDIX. The following epiphyte species list includes plant size and number of trees where epiphytes were found after ground-based (ground) and climbing-based (canopy) observations in three vegetation types (pasture, riparian, and forest). Plant sizes are based on Mickel and Beitel (1988), Hietz and Hietz-Seifert (1994), and on our own observations. Figures in parentheses are the number of trees sampled.

Epiphyte species	Epiphyte size (m)	Pasture (17 trees)		Riparian (42 trees)		Forest (49 trees)	
		Ground	Canopy	Ground	Canopy	Ground	Canopy
PTERIDOPHYTES							
Aspleniaceae							
Asplenium sp. (1)	0.20–0.40	0	0	1	1	0	0
Asplenium sp. (2)	0.20–0.40	0	0	1	1	0	0
Asplenium sp. (3)	0.20–0.40	0	0	3	3	0	0
Grammitidaceae							
Grammitis leptostoma (Fée) F. Seym.	0.12–0.15	0	0	0	0	3	3
Hymenophyllaceae							
Hymenophyllum polyanthos (Sw.) Sw.	0.03–0.10	0	0	1	1	0	0
Trichomanes capillaceum L.	0.10–0.10	0	0	0	0	1	1
Lomariopsidaceae							
Elaphoglossum lonchophyllum (Fée) T. Moore	0.24–0.74	1	1	0	0	4	4
Elaphoglossum glaucum T. Moore	0.20–0.62	0	0	0	0	0	1
Elaphoglossum guatemalense (Klotzsch) T. Moore	0.30–0.60	0	0	0	0	1	2
Elaphoglossum vestitum (Schldl. & Cham.) T. Moore	0.25–0.60	0	0	10	10	7	7
Peltapteris peltata (Sw.) C. V. Morton	0.03–0.10	0	0	1	1	1	1
Lycopodiaceae							
Huperzia linifolia (L.) Trevisan	0.13–0.40	0	0	1	1	2	5
Huperzia myrsinites (Lam.) Trevisan	0.20–0.55	0	0	5	6	2	2
Hupertzia pringlei (Underw. & F. E. Lloyd) Holub.	0.20–0.70	0	0	1	1	0	1
Huperzia taxifolia (Sw.) Trevisan	0.20–0.60	0	0	6	8	3	5
Ophioglossaceae							
Botrychium virginianum (L.) Sw.	0.25–0.75	0	0	0	1	0	0
Polypodiaceae							
Pecluma alfredii (Rosenst.) M. G. Price	0.20–0.55	10	10	17	17	7	8
Phlebodium aerolatum (Humb. & Bonpl. ex Willd.) J. Sm.	0.20–1	15	15	35	40	39	45
Pleopeltis angusta var. *stenolama* (Fée) Farw.	0.6–0.10	1	4	7	15	7	15
Pleopeltis crassinervata (Fée) T. Moore	0.09–0.20	8	11	9	25	16	32
Pleopeltis mexicana (Fée) Mickel & Beitel	0.10–0.15	8	11	6	11	13	20
Polypodium furfuraceum Schldl. & Cham.	0.23–0.50	5	8	11	21	6	15
Polypodium lepidotrichum (Fée) Maxon	0.30–0.65	4	5	2	5	8	16
Polypodium loriceum L.	0.15–0.85	0	0	8	9	14	15
Polypodium plebeium Schldl. & Cham.	0.12–0.35	6	12	22	37	28	37
Polypodium puberulum Schldl. & Cham.	0.30–0.60	0	0	0	6	0	3
Psilotaceae							
Psilotum complanatum Sw.	0.10–0.50	0	0	1	1	0	0
Selaginellaceae							
Selaginella martensi Spring	0.15–0.25	0	0	1	1	1	1
Vittariaceae							
Vittaria graminifolia Kaulf.	0.10–0.20	0	0	1	1	3	4
SPERMATOPHYTES							
Araceae							
Anthurium scandens (Aubl.) Engl.	>1	4	8	20	25	16	22
Philodendron advena Schott	1–>5	0	0	3	3	6	6
Syngonium sagittatum G. S. Bunting	1–4	0	0	2	2	3	3
Araliaceae							
Oreopanax capitatus (Jacq.) Decne. & Planch.	1–3	1	2	14	14	3	4
Oreopanax liebmani Marchal	1–3	0	0	1	2	1	1

APPENDIX. Continued.

Epiphyte species	Epiphyte size (m)	Pasture (17 trees)		Riparian (42 trees)		Forest (49 trees)	
		Ground	Canopy	Ground	Canopy	Ground	Canopy
Oreopanax xalapensis (Kunth) Decne. & Planch.	1–3	0	0	1	1	0	0
Oreopanax sp.	1–3	1	1	0	0	0	0
Arecaceae							
Chamaedorea tepejilote Liebm. ex Mart.	0.30–>1	0	0	0	0	1	1
Bromeliaceae							
Catopsis nitida (Hook.) Griseb.	0.30–0.40	2	8	3	8	18	29
Catopsis nutans (Sw.) Griseb.	0.10–0.15	0	8	25	32	7	13
Catopsis sessiliflora (Ruiz & Pav.) Mez	0.10–0.15	15	17	3	17	14	28
Tillandsia butzii Mez	0.20–0.30	13	16	29	35	42	47
Tillandsia deppeana Steud.	>1.3	1	1	0	0	0	0
Tillandsia foliosa M. Martens & Galeotti	>1.3	1	2	0	0	0	1
Tillandsia ghiesbregthii Baker	>1.2	4	12	3	18	18	35
Tillandsia gynmnobotrya Baker	0.70–1	0	0	1	2	9	12
Tillandsia juncea (Ruiz & Pav.) Poir.	0.30–0.50	2	8	0	3	4	7
Tillandisa kirchoffiana Wittm.	>1.2	14	16	34	40	40	46
Tillandsia limbata Schltdl.	>1.2	0	2	0	0	0	0
Tillandsia lucida E. Moren ex Baker	>1.1	3	5	0	5	0	0
Tillandsia multicaulis Steud.	0.30–0.50	17	17	35	40	36	46
Tillandsia punctulata Schltdl. & Cham.	0.40–0.50	16	17	30	33	26	36
Tillandsia shiedeana Steud.	0.15–0.25	1	4	0	5	0	11
Tillandsia sp. (1)	0.15–0.25	0	4	0	4	1	5
Tillandsia sp. (2)	0.50–0.70	0	2	0	6	0	1
Tillandsia tricolor Schldl. & Cham.	0.40–0.70	0	3	0	2	1	4
Tillandsia usneoides (L.) L.	0.10–>1	0	0	0	2	0	0
Tillandsia viridiflora (Beer) Baker	>1.5	0	0	8	8	21	24
Commelinaceae							
Gibasis sp.	0.2–0.5	0	0	5	5	0	0
Orchidaceae							
Acineta barkeri (Bateman) Lindl.	0.60–1	3	3	6	6	5	6
Arpophyllum sp.	0.25–0.45	0	0	0	0	1	2
Barbosella prorepens (Rchb. f.) Schltr.	<0.05	0	0	1	1	0	0
Brassia verrucosa Lindl.	0.30–0.40	2	2	4	5	1	3
Chisys leavis Lindl.	0.20–0.30	0	1	0	0	1	1
Coelia macrostachya Lindl.	0.55–0.70	0	0	2	2	2	2
Comparettia falcata Poepp. & Endl.	0.05–0.15	1	1	1	2	0	1
Dichaea glauca (Sw.) Lindl.	0.25–0.40	0	1	8	9	12	14
Dichaea intermedia Ames & Correll	0.10–0.30	0	0	1	1	1	1
Dichaea neglecta Schltr.	0.10–0.30	0	0	5	6	2	3
Dichaea sp.	0.10–0.15	0	0	0	1	3	3
Elleanthus cynarocephalus (Reichb. f.) Reichb. f.	>1	0	0	2	2	3	3
Encyclia polybulbon (Sw.) Dressler	<0.05	0	0	1	1	1	2
Encyclia sp.	0.30–0.50	0	1	0	0	0	1
Epidendrum laucheanum Rolfe ex Bonhof	0.20–0.30	0	0	1	1	0	0
Epidendrum parkinsonianum Hook.	0.30–>1	0	0	0	0	0	1
Epidendrum polyanthum Lindl.	>1	0	0	0	0	3	3
Epidendrum veroscriptum Hágsater	>1	0	0	2	2	1	1
Isochilus sp.	0.20–0.30	0	0	0	0	1	1
Isochilus unilateralis B. L. Rob.	0.50–0.70	1	1	1	1	7	7
Jacquiniella globosa (Jacq.) Schltr.	0.05–0.15	0	0	0	2	2	8
Jacquiniella teretifolia (Sw.) Britton & P. Wilson	0.15–0.30	1	3	7	12	17	22
Laelia anceps Lindl.	0.15–0.30	0	0	0	0	0	1
Lycaste deppei (G. Lodd.) Lindl.	0.15–0.40	0	0	2	3	0	1
Malaxis excavata (Lindl.) Kuntze	0.10–0.20	0	0	0	0	0	1
Maxillaria cucullata Lindl.	0.20–0.50	0	0	0	0	4	5
Maxillaria meleagris Lindl.	0.20–0.50	1	1	0	0	2	2
Maxillaria variabilis Bateman & Lindl.	0.15–0.30	0	0	0	0	1	1

APPENDIX. Continued.

Epiphyte species	Epiphyte size (m)	Pasture (17 trees)		Riparian (42 trees)		Forest (49 trees)	
		Ground	Canopy	Ground	Canopy	Ground	Canopy
Pleurothallis aff. *tribuloides* (Sw.) Lindl.	<0.10	0	0	0	0	0	2
Pleurothallis pachyglossa Lindl.	0.15–0.30	0	0	1	3	15	15
Pleurothallis platystilis Schltr.	0.10–0.20	0	0	9	9	1	4
Pleurothallis tubata (G. Lodd.) Steud.	0.10–0.15	0	0	1	1	0	0
Prosthechea ochracea (Lindl.) W. E. Higgins	0.12–0.25	0	0	1	1	1	2
Prosthechea vitellina (Lindl.) W. E. Higgins	0.15–0.40	1	3	1	5	13	24
Rhynchostele cordatum (Lindl.) Soto-Arenas & Salazar	0.25–0.35	0	0	0	1	0	0
Scaphyglottis sp.	0.10–0.40	0	2	1	1	0	0
Xylobium foveatum (Lindl.) G. Nicholson	0.10–0.25	0	0	1	1	0	0
Piperaceae							
Peperomia aff. *alata* Ruiz & Pav.	0.10–0.20	5	5	23	24	5	8
Peperomia galioides Kunth	0.10–0.20	5	6	6	8	3	6
Peperomia pseudoalpina Trel.	0.15–0.30	0	0	10	11	18	20
Peperomia aff. *quadrifolia* (L.) Kunth	0.05–0.10	0	0	1	1	8	10
Peperomia sp.	<0.05	0	1	2	6	3	5
Rubiaceae							
Unknown	0.10–0.15	0	0	1	1	0	0